

EMIGRATION RAIDS BY SLAVE-MAKING ANTS: A RAPID-TRANSIT SYSTEM FOR COLONY RELOCATION (HYMENOPTERA: FORMICIDAE)

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INTRODUCTION

Polyergus lucidus Mayr is an obligate slave-making ant, found throughout north temperate regions of the world. Their slave raids are dramatic events in which columns of highly aroused workers penetrate nests of the related ant genus *Formica*, and carry the target colony's pupae back to their own nest (Marlin 1969; Talbot 1967). Although many of these pupae are consumed, varying numbers are reared through eclosion and become permanent members of the mixed-species nest. During the evolution of social parasitism, *Polyergus* workers lost the ability to participate in the ordinary chores of foraging, nest maintenance, and brood rearing, all of which are left to the *Formica* slaves.

Raiding behavior in *Polyergus* has only been reported in the context of slave raids, or of intraspecific territorial raids (Topoff et al. in preparation). Field observations of colonies in late summer, however, have revealed an entirely new function of raiding behavior: the rapid transport of colony members during emigrations to new nests at the end of the slave-raiding season. During such colony movements, the low level of mixed-species ant traffic is periodically interrupted by the abrupt emergence of *Polyergus* workers, and their formation into a well-organized swarm. The *Polyergus* workers promptly "raid" the old nest, and transport adult *Formica* individuals to the new site. For such group processes, occurring in the context of nest relocation, we propose the term "emigration raid."

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METHODS

Emigration raids were observed in three mixed colonies of *P. lucidus* and *F. schaufussi* Mayr, located in a pine-barrens habitat in North Centereach, Long Island, N.Y. The most detailed data were collected from a colony monitored continuously from July through September, 1976. The emigrations occurred on September 19 and 20, as the colony moved to a previously-constructed nest, 5.9 m southwest of the old site. Movements of individual ants shuttling between nests were monitored with hand-held tally counters. Callow age was estimated by comparing their degree of pigmentation with individuals of known age in laboratory nests (Kwait 1982).

RESULTS AND DISCUSSION

During the morning and early afternoon of each day, the population characteristics of the emigrations were similar to those described for *Polyergus* nest movements that occasionally occur in the spring (Marlin 1971). Thus, only *Formica* workers functioned as transporters, carrying adults and brood of both species to the winter nest (Fig. 1). As the afternoon progressed, however, several *P. lucidus* workers periodically joined the emigration. Although these *Polyergus* individuals made 5–23 trips between nests, the important point to note is the relatively low level of overall activity during most of the afternoon (Fig. 2A). But starting about 1600 hrs (EDT), at approximately the same time as the onset of slave raids earlier in the season (compare Fig. 2A and 2B), groups of 30–69 callow and mature- adult *Polyergus* abruptly surged out of the new nest and formed into an organized swarm. This raid swarm backtracked and penetrated the old nest, and after several minutes the *Polyergus* workers emerged carrying nestmates (Table 1). On both emigration days, the first emigration raid was promptly followed by a second raid (Fig. 2A). Activity levels for both species then dropped abruptly, as they typically do during slave raids on freeliving colonies of *Formica*.

Aside from our field observations on emigration raids, the only other reference to *Polyergus* carrying adult *Formica* individuals is Huber's (1810) study in Switzerland, of an emigration into an abandoned *Formica* nest. A more recent observation of comparable behavior stems from studies of *P. breviceps*-*Formica gnava* mixed colonies in a desert habitat in southeastern Arizona (Topoff et al. in

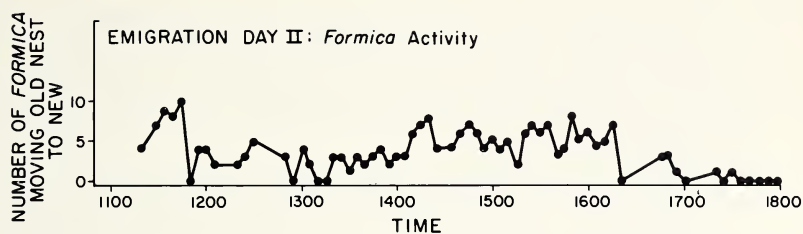


Figure 1. Activity of *Formica schaufussi* during colony emigration. Most of the workers are carrying adults and brood of *Polyergus* and *Formica* to the winter nest.

preparation). On August 14, 1981, colony #1 raided another mixed nest (#2), 30 m to the east. Fighting between resident and intruding *Polyergus* workers was minimal, and only about 11 pupae were captured. Early in the afternoon on August 15, *Polyergus* workers emerged from colony #2 and backtracked over the previous day's trail towards mixed colony #1. At 1715 hrs (MST), traffic again reversed direction, as hundreds of *Polyergus* workers penetrated nest #2. This time, however, the *Polyergus* emerged carrying hundreds of *Formica* brood, callows, and mature-adult individuals. All of the adult *Formica* being transported had their appendages closely appressed to the body, in the "pupa-like" position that is typical during social carrying behavior (Möglich and Hölldobler 1974). The adult *Formica* were carried into mixed nest #1, and none had re-emerged by the end of the observation period at sunset.

The description by Huber (1810) of adult *Formica* transport by *Polyergus* clearly took place within the context of a colony emigration. Our observation of similar behavior by *P. breviceps* is more difficult to interpret, but we suggest that it occurred in the context

Table 1. Quantitative Description of Emigration Raids

Date	Raid #	Time	<i>Polyergus</i> on raid	Adult <i>Formica</i> retrieved	<i>Formica</i> pupae retrieved
9/19/76	1	1525	56	37	3
	2	1625	45	35	0
9/20/76	1	1620	69	30	0
	2	1703	30	15	0

of colony reunification shortly after division by budding. The important point in both cases, however, is that adult transport of *Formica* by *Polyergus* took place in a staggered, prolonged, emigration-type column, without the intervention of an abrupt, short-lived, and full-scale raid.

That the *P. lucidus* emigration raids reported in the present study are fundamentally similar behavioral processes to their slave raids is evidenced by the congruence of several parameters, including: (1) the immediate organization of the emerging workers into an organized swarm; (2) the time of raid onset; (3) the occurrence of multiple raids; and (4) the participation of recently-eclosed *Polyergus* callows. The number of *Polyergus* workers in the emigration raids was lower than that characteristic of most slave raids. This difference is probably not significant, because it is known that even slave-raid participants decrease to as few as 13–50 individuals towards the end of the raiding season (Talbot 1967). Nevertheless, the social context of an emigration does produce at least one major difference in the behavior of the *Polyergus* workers. During emigration raids, it is principally *Formica* adults that are carried by the *Polyergus*. Because these adult slaves were reared from the pupal stage in the chemical and tactile environment of the mixed nest, the communicatory basis for social carrying behavior is well established. During slave raids, by contrast, *Formica* adults respond to the intruding *Polyergus* by exhibiting various forms of withdrawal behavior (Wilson 1971). As a result, it is principally *Formica* pupae and callows that are retrieved during slave raids.

Emigration behavior with adult transport is common in many ant species (Smallwood 1982), including free-living colonies of *Formica schaufussi*. Because *F. schaufussi* is considered related to *Polyergus*, emigrations probably pre-date the evolution of slave-raiding behavior. The secondary use of raiding behavior for *Polyergus* colony relocation represents an adaptive evolutionary transition, consistent with Simpson's (1958) principle of "transformation." Accordingly, when changes at any level of organization take place during a species' evolution, previously existing adaptations are often remodeled and eventually serve new functions. Because group raiding in *Polyergus* involves a complex recruitment process specialized for the efficient retrieval of other ants, it is clearly advantageous for the colony to utilize the process in all appropriate behavioral contexts.

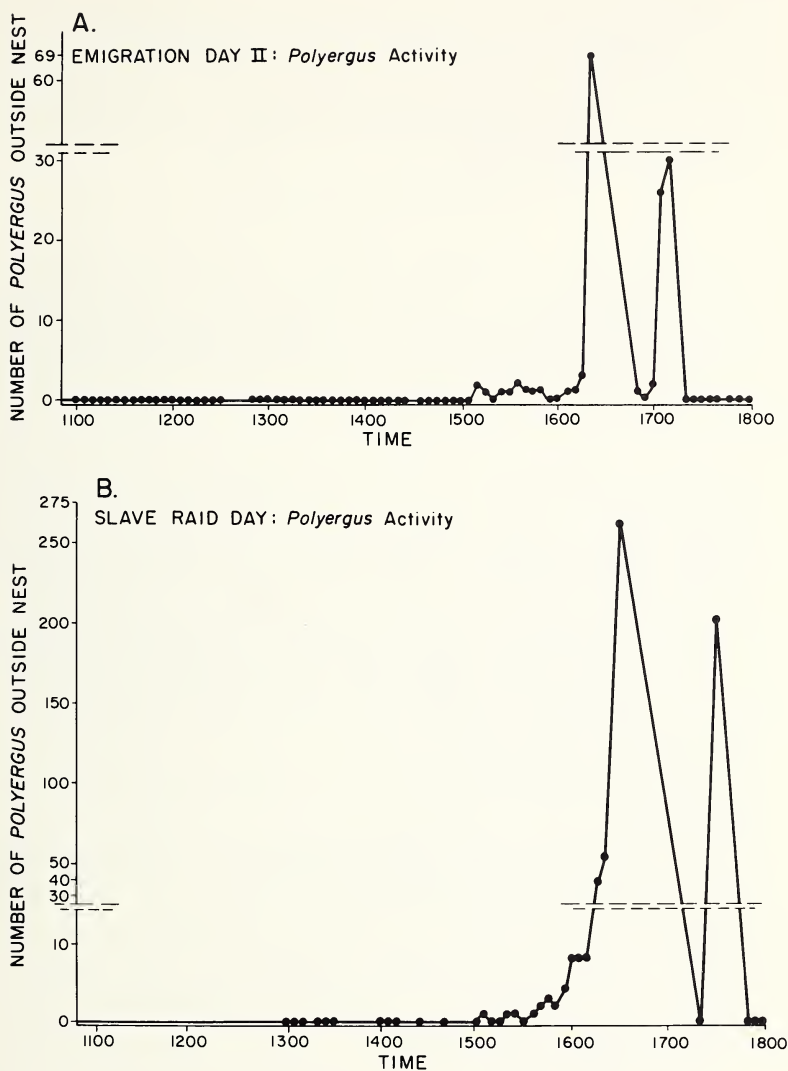


Figure 2. (A) Activity of *Polyergus lucidus* during colony emigration. The two consecutive peaks in afternoon activity represent emigration raids conducted on the old nest by *Polyergus* workers that were transported to the new nest by *Formica* individuals. (B) Activity of *P. lucidus* during typical slave-raid day. Note the similarity in timing of slave raids and emigration raids.

The rapid transport by *Polyergus* of adult *Formica* slaves to an overwintering site shortens the emigration time during a season characterized by increasingly unfavorable weather, and quickly relocates the *Formica* slaves to the new nest where they are needed for overall colony maintenance.

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